ALLELIC VARIATION IN THE AMPHITROPICAL DISJUNCT *LYCURUS SETOSUS* (POACEAE: MUHLENBERGIINAE)

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ABSTRACT

Lycurus consists of three species, all with paired, single-flowered spikelets (the lower is short pedicellate and usually staminate, the upper long pedicellate and perfect). *Lycurus setosus* occurs in the southwestern USA, northern Mexico, northwestern Argentina, and Bolivia. Allozyme data were used to evaluate genetic diversity within and among populations of this amphitropical disjunct species. Electrophoretic examination of 18 putative enzyme loci in 13 populations revealed high levels of genetic variation (P ranging from 0.43 to 0.79; H from 0.31 to 0.62) and high levels of genetic diversity (F ranging from -0.38 to -1.00). All populations possess high levels of heterogeneity (F_{is} approaching -1, mean of -0.723) and exhibit lower levels of genetic fixation among populations (F_{ST} mean of 0.256). A comparison of genetic identity values among populations from North and South America indicates that the genetic variation is greater ($I = 0.89$) in North America than in South America ($I = 0.94$), and populations from South America lack six alleles found in the North American populations. There was one unique allele found in populations from South America. It seems likely that *Lycurus setosus* has recently dispersed to South America because the populations there contain less genetic variation.

RESUMEN

Lycurus consiste en tres especies, todas con espiguillas dispuestas en pares, flosculo único (el basal brevemente pedicelado y usualmente estaminado, y el distal largamente pedicelado y perfecta). *Lycurus setosus* habita en el suroeste de Estatos Unidos, norte de México, noreste de Argentina y Bolivia. Mediante el análisis de alozimas se evaluó la diversidad genética dentro y entre poblaciones de esta especie disjunctiva anfitropical. El exámen electroforético de 18 loci putativos enzimáticos en 13 poblaciones, reveló altos niveles de variación genética (P varía de 0.43 a 0.79; H varía de 0.31 a 0.62) y altos niveles de diversidad genética (F varía de -0.38 a -1.00). Todas las poblaciones poseen altos niveles de heterogeneidad dentro de las mismas poblaciones (F_{IS} cerca -1, media de -0.723) y exhiben bajos niveles de fijación genética entre poblaciones (F_{ST} media de 0.256). Una comparación de valores de identidad genética entre poblaciones de Norte y Sur América indican que la variación genética es mayor ($I = 0.89$) en Norte America que en Sur América ($I = 0.94$), y poblaciones de Sur América carecen de seis alelos encontrados en poblaciones de Norte América. Se halló un único alelo en poblaciones de Sur Americanas. Probablemente, *Lycurus setosus* ha sido recientemente dipersado hacia Sur América porque esta poblaciones contienen menos variacion genética.

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Lycurus Kunth consists of three species restricted to the New World: *L. phalaroides* Kunth, *L. phleoides* Kunth, and *L. setosus* (Nutt.) C. Reeder. The amphitropical disjunct, *Lycurus setosus,* occurs in the southwestern U.S. and northern Mexico, and again in northwestern Argentina and Bolivia. This species was originally described by Nuttall (1848) from plants collected in the vicinity of Santa Fe, New Mexico, as a distinct genus *Pleopogon setosum* Nutt. Beal (1896) recognized this taxon as *Lycurus phleoides* Kunth var. *glaucifolius* Beal. Later authors placed this species as a synonym of *L. phleoides* (Hitchcock 1913, 1937, 1939). It was not until C. Reeder (1985) revised *Lycurus* that we came to recognize *L. setosus* as a third species in the genus.

The genus is characterized by having paired, single-flowered spikelets; the lower short, pedicellate and usually staminate, occasionally sterile or perfect, the upper long pedicellate and perfect (Peterson et al. 1997). The first glume is 2- or 3-nerved with two awns, 3–7 mm long and the lemma is 3-nerved and awned. *Lycurus setosus* can be differentiated from the other two species in the genus by having leaf blades terminating in slender seta 0.5–10(12) mm long and acute to acuminate ligules 3–10 mm long.

Upon describing the genus with two species, Kunth (1816) suggested *Lycurus* was similar to *Phleum* L. in habit, with affinities to *Aegopogon* Humb. & Bonpl. ex Willd. Based on anatomical characteristics, Sánchez and Rúgolo de Agrasar (1986) suggested *Lycurus* be aligned with *Aegopogon* and *Tragus* Haller f. (tribe Zoysieae). Sánchez and Rúgolo de Agrasar (1986) also pointed out the anatomical similarity between *Erioneuron* Nash (tribe Eragrostideae) and *Lycurus.* Based upon morphological similarities, Mez (1921) transferred *Muhlenbergia shaffneri* E. Fourn., considered a synonym of *Muhlenbergia depauperata* Scribn., to *Lycurus. Muhlenbergia depauperata* and *M. brevis* C. O. Goodd. share many morphological features with *Lycurus,* most importantly: paired spikelets, 2-nerved lower glumes with two awns, and 3-nerved lemmas (Peterson and Annable 1991). Pilger (1956) erected the subtribe Lycurinae, which included *Lycurus* and *Pereilema* J. Presl. Clayton and Renvoize (1986) and Valdes-Reyna and Hatch (1991) took the traditional view and place *Lycurus* in the subtribe Sporobolinae, along with *Calamovilfa* (A. Gray) Hack. ex Scribn. & Southw., *Crypsis* Aiton, *Muhlenbergia* Schreb., *Pereilema,* and *Sporobolus* R. Br. Based on chloroplast DNA evidence, *Lycurus* appears to be firmly embedded in the subtribe Muhlenbergiinae, subfamily Chloridoideae, along with *Bealia* Scribn., *Blepharoneuron* Nash, *Chaboissaea* E. Fourn., *Muhlenbergia,* and *Pereilema* (Duvall et al. 1994; Peterson et al. 1995, 1997).

The origin of the Chloridoideae (=Eragrostoideae, *sensu* Pilger 1954, 1956) appears to be in southwestern Africa, where the climate

is extremely arid, summer rainfall is common, and mean winter temperature is above 10°C (Hartley and Slater 1960). Chloridoid centers of diversity occur in southwestern Africa, northcentral (Tibesti, Sahara) Africa, and northwestern USA/northern Mexico (Clayton 1975; Hartley and Slater 1960). This wide distributional pattern suggests that the subfamily is an old one and that subsequent radiation from the African continent has occurred (Hartley and Slater 1960).

Although there is some doubt as to the specific taxon surveyed, chromosome counts for *Lycurus setosus* indicate that it is tetraploid ($2n = 40$) with a base chromosome number of $x = 10$ (Avdulov 1931; Gould 1964, 1965; J. Reeder 1967, 1971, 1977). The U.S. National Herbarium (US) has four specimens of *L. setosus* from Chihuahua and Durango, Mexico, collected by Reeder and Reeder (4877, 4884, 4890, 4898) that indicate a chromosome count of $2n = 40$.

The present study, the first analysis of soluble enzymes in *Lycurus,* was initiated to estimate the genetic diversity within and among populations of *L. setosus.* We also hoped to gain new insights into the phytogeographical history and evolutionary processes operating among populations with amphitropical disjunct distributions. Similar studies of allozyme variation in *Bealia mexicana* Scribn., *Chaboissaea atacamensis* (Parodi) P. M. Peterson and Annable, *C. decumbens* (Swallen) Reeder and C. Reeder, *C. ligulata.* E. Fourn., *C. subbiflora* (Hitchc.) Reeder and C. Reeder, *Muhlenbergia argentea* Vasey, *M. lucida* Swallen, *M. torreyi* (Kunth) Hitchc. ex Bush, and *Scleropogon brevifolius* Phil. have revealed high intraspecific variability (*H* ranging from 0.19 to 1.00) and high levels of genetic diversity (*F* ranging from 0.073 to −1.000) (Peterson and Columbus 1997; Peterson and Herrera A. 1995; Peterson and Ortíz-Diaz in preparation; Peterson et al. 1993).

Methods

Thirteen populations representing 365 individuals were sampled from throughout the geographic range of *Lycurus setosus* (Table 1). Fresh leaf blades were collected in the field, placed in 3.6 or 5.0 ml cryotubes (NUNC), and frozen on site in liquid nitrogen.

Sample preparation and electrophoresis of enzymes followed the general methodology of Morden et al. (1987). Approximately 300 mg of mature tissue from each plant was homogenized in up to 25 drops of grinding buffer together with about 50 mg of sea sand to enhance disruption of cells. Extracts were absorbed into 2 × 11 mm Whatman filter paper wicks and stored at −80°C. Electrophoresis was conducted in the four gel/electrode buffer systems (L, M, N, T) as described in Morden et al. (1987). Starch concentration was mod-

TABLE 1. FIELD COLLECTIONS OF *LYCURUS SETOSUS* ANALYZED BY ENZYME ELECTROPHORESIS. Vouchers deposited at US.

ARGENTINA. **Juyuy:** Depto. Humahuaca: 20 km N of Humahuacaon Hwy 9 towards Tres Cruces, 17 Mar. 1991, *Peterson & Annable 11762.* **Mendoza:** Depto. Lujan de Cuyo, 12 km SW of Potrerillos, 26 Feb. 1991, *Peterson & Annable 11439.* **Salta:** Depto. La Poma, 4 km N of Saladillo on Hwy 40, 15 Mar. 1991, *Peterson & Annable 11746.*. Depto. San Carlos, just E of Isonza and 26 km N of Amblayo, 13 Mar. 1991, *Peterson & Annable 11724.* **San Juan:** Depto. Zonda, 37 km SW of Zonda at Estancia Maradona, 29 Feb. 1991, *Peterson & Annable 11513.* **Tucuman:** Depto. Tafi del Valle, 30 km SE of Amaicha del Valle on Hwy 307, 8 Mar. 1991, *Peterson & Annable 11622.*

MEXICO. **Sonora:** Sierra El Gato, 5.7 mi E of Huachinera, 9 Oct. 1992, *Peterson & Annable 12350.*

U.S.A. **Arizona:** Coconino Co., 6 mi NW of Ash Fork on Canyon Road (39) below Antolini, 28 Sep. 1992, *Peterson & Annable 12174.* Gila Co., 3.7 mi S of Young on Hwy 288 towards Globe, 30 Sep. 1992, *Peterson & Annable 12218.* Pima Co., Santa Rita Mountains, 4.8 mi W of Hwy 83 on Forest Service 231 and 0.2 mi W on Forest Service 4053, 1 Oct. 1992, *Peterson & Annable 12246.* Yavapai Co., 8.7 mi SW of Jerome on Hwy 89A, 28 Sep. 1992, *Peterson & Annable 12184.* **New Mexico:** Grant Co., Burro Mountains, 0.3 mi N of Hwy 90 on Mill Canyon Road (Forest Service 859), 4 Oct. 1992, *Peterson & Annable 12299.* Hidalgo Co., Peloncillo Mountains, 10 mi W of Hwy 338 on Forest Service 63 in Clayton Draw, 5 Oct. 1992, *Peterson & Annable 12320.*

ified to improve gel handling and improve resolution; all gels consisted of Sigma hydrolyzed potato starch at concentrations of 10.6%, 12.0%, 11.5%, and 12.0% for the L, M, N, and T systems, respectively. For each population, samples from all individuals were included together on the same gel. Selected individuals from different populations were then analyzed together for purposes of interspecific and interpopulational comparisons.

Gels were sliced and stained for the following 14 enzymes: aspartate aminotransferase (AAT), aconitase (ACO), adenylate kinase (ADK), aminopeptidase (AMP), fructokinase (FRK), glutamate dehydrogenase (GDH), glutamate-pyruvate transaminase (GPT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SAD), and triose phosphate isomerase (TPI). Banding pattern interpretations are based on known subunit structure and conserved number of loci at the diploid level. Only the faster migrating bands of IDH, assumed to be the nuclear-encoded plastid form were surveyed (Gottlieb 1982; Weeden and Wendel 1989). Loci were designated sequentially with the most anodally-migrating locus designated 1, the next 2, and so on. Alleles were designated sequentially with the most anodally-migrating allele given an *a*, the next *b*, and so on.

Values for Nei's (1972) genetic identity (*I*) and distance measures

TABLE 2. GENETIC VARIATION IN POPULATIONS OF *LYCURUS SETOSUS*: sample size (n); mean number of alleles per locus (A); mean proportion of polymorphic loci (P); 95% criterion, mean heterozygosity (H), direct count estimate; and mean fixation index (F).

Collection No.	n	A	P	H	F
11439	29.0	1.4	42.9	0.429	−1.000
11513	30.3	1.9	71.4	0.311	−0.390
11622	27.0	1.8	57.1	0.532	−0.833
11724	29.0	1.8	57.1	0.520	−0.789
11746	30.0	1.7	64.3	0.569	−0.778
11762	30.0	1.8	64.3	0.417	−0.583
12174	28.0	1.9	57.1	0.372	−0.527
12184	28.0	1.8	57.1	0.520	−0.722
12218	27.0	2.1	78.6	0.450	−0.444
12246	28.0	1.9	78.6	0.615	−0.607
12299	27.9	1.7	57.1	0.334	−0.413
12320	27.1	1.9	78.6	0.398	−0.379
12350	23.0	2.0	71.4	0.385	−0.433
Total Means	28	1.8	64	0.45	−0.61

were computed for pairwise comparisons using BIOSYS-1 (Swofford and Selander 1989). Although all these populations are probably tetraploid in origin, an initial BIOSYS-1 run was undertaken to measure each population's genetic variability and to compute genetic identities (Nei 1972). Standard measures of genetic variation (Table 2) were computed including mean number of alleles per locus (*A*), proportion of polymorphic loci (*P*), mean heterozygosity (*H*), and mean fixation index (*E*) which measures the deviation of genotypic proportions from Hardy-Weinberg expectations (Wright 1965). The distribution of genetic variation was determined using F-statistics where F_{IS} is the fixation index within populations, F_{IT} is the overall fixation index or inbreeding coefficient, and F_{ST} measures the degree of differentiation among populations (Wright 1965, 1969; Jain and Workman 1967). The patristic distance matrix was calculated using the Prevosti distance index (Wright 1978) and after optimization of branch lengths, a corresponding phenogram (Fig. 1) using the Wagner procedure was produced (Swofford and Selander 1989).

RESULTS

Eleven enzyme systems encoded by 18 putative loci were consistently scorable by starch gel electrophoresis: AAT-1, AAT-2, ACO-1, ACO-2, AMP-1, AMP-2, GDH, GPT, IDH, PGD, PGI-1, PGI-2, PGM-1, PGM-2, SAD-1, SAD-2, TPI-1, TPI-2. Several enzymes or putative loci, viz., ADK, FRK, MDH, and PGD-2 were not scorable due to faint or inconsistent staining. Allele frequencies

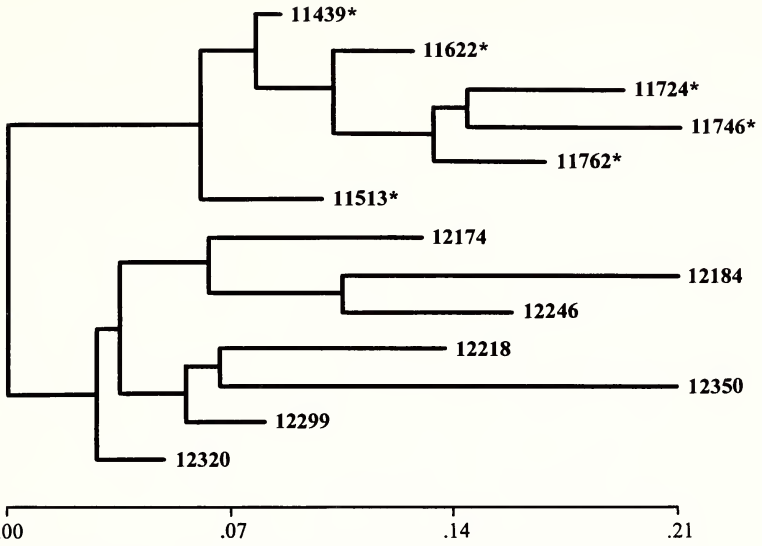

FIG. 1. Phenogram showing genetic distance among populations of *Lycurus setosus*. Correlation coefficient = 0.841; length = 0.971; numbers refer to population collections given in Table 1; populations from South America are marked with an asterisk; scale indicates distance from midpoint.

for all 13 populations surveyed appear in Appendix 1. The number of alleles per polymorphic locus ranged from two in AAT-1, AAT-2, AMP-1, AMP-2, GDH, GPT, PGD, PGM-1, PGM-2, TPI-1, and TPI-2 to six in PGI-1. The following loci were fixed for a single allele for all populations: AMP-1 and AMP-2. The largest number of alleles per locus in a population was four, occurring in PGI-1 (population *11513*). There was no evidence of duplicated loci, however, AAT-1, AAT-2, GDH, and GPT were fixed for a pair of different alleles and removed from the genetic analysis.

The sample size (n) per population ranged from 23 to 30 individuals and the mean number of alleles per locus (*A*) within populations ranged from 1.4 to 2.1 (Table 2). The percentage of polymorphic loci (*P*) ranged from 0.429 to 0.786 and the mean heterozygosity (*H*), direct count estimate, ranged from 0.311 to 0.615, indicating a high level of heterozygosity at most polymorphic loci (Table 2). The mean fixation index (F) within populations, or inbreeding coefficient, ranged from −0.38 to −1.00. Genetic variability as measured in pooled populations from North and South America was: $A = 1.7$, 1.9; $P = 60$, 68; $H = 0.46$, 0.44 (Table 3).

There were 45 alleles recorded in the North American populations and 40 in the South American populations (Appendix 1, Table 3). One unique allele was detected in each of four populations *11513*

TABLE 3. GENETIC VARIABILITY IN NORTH AND SOUTH AMERICAN POPULATIONS OF *LYCURUS SETOSUS*: number of populations sampled (n); mean number of alleles per locus (A); mean proportion of polymorphic loci (P); 95% criterion, mean heterozygosity (H), direct count estimate; and alleles in common and unique (u).

Country	n	A	P	H	Alleles (u)
South America	6	1.7	59.5	0.463	40 (1)
North America	7	1.9	68.4	0.439	45 (6)

(PGI-1-b), *12184* (PGI-2-c), *12320* (TPI-1-a), and *12350* (SAD-1-a). Two of these unique alleles were found in single individuals in populations *11513* and *12320*; PGI-2-c (*12184*) was found in two individuals and SAD-1-a (*12350*) was found in eight individuals. In North America all seven populations shared alleles PGI-1-a & d and two populations (*12174, 12350*) shared allele SAD-2-a. None of these three alleles was present in South American populations. In summary, a total of six alleles are exclusively shared by North American populations and a one allele is unique in South America (Table 3).

Partitioning of genetic diversity, or the fixation of alleles at different hierarchical levels, within and among populations of *Lycurus setosus* was calculated using *F*-statistics where the fixation index within populations (F_{IS}) ranged from −0.019 to −0.927 (mean −0.723). The amount of genetic diversity among populations (F_{ST}) ranged from 0.017 to 0.456 (mean 0.256). The overall fixation index (F_{IT}) ranged from 0.008 to −0.758 (mean −0.281). The primary component of F_{IT} was F_{IS}, i.e., the F_{ST} values were much smaller, indicating greater heterogeneity within populations than among them.

A phenogram (Fig. 1) summarizes the interpopulational relationships based on genetic distance values. Six populations from South America are differentiated on a single branch at the 0.38 level or distance from root, whereas seven populations from North America are differentiated on a single branch at the 0.20 level. These two branches separating the North from the South American populations are then joined near the base at the 0.009 level.

Mean genetic identities (Nei 1972) among populations were quite variable ranging from 0.718 between population *12184* and *12350* (both from North America), to 0.978 between population *12299* and *12320* (both from North America). The mean genetic identity for all 13 populations was 0.89. A comparison of identity values among populations from North and South America indicates that the genetic variation is greater ($I = 0.89$) in North America than in South America ($I = 0.94$).

Discussion

All populations of *Lycurus setosus* examined in this study show high levels of genetic variation comparable to that found in outcrossing plant species (Hamrick and Godt 1989; Hamrick et al. 1979). This is reflected in the high mean values for all populations for proportion of polymorphic loci of 0.64, heterozygosity of 0.45, and negative F values of -0.61. All of these values indicate a consistent excess of heterozygotes (Table 2). All populations possess high levels of heterogeneity within populations (F_{IS} approaching -1, mean of -0.723) and exhibit lower levels of genetic fixation among populations (F_{ST} mean of 0.256).

Since the phenogram (Fig. 1) was computed using genetic distance it mirrors the results inferred from genetic identities. Clearly, populations from South America form a more compact group reflecting a lower genetic variability. However, population *11513* from San Juan, Argentina, is quite variable (mean number of alleles per locus, $A = 1.9$, and proportion of polymorphic loci, $P = 71.4$) and similar to North American populations.

Genetic identities values indicated that populations from South America ($I = 0.94$) were more similar to each other than those from North America ($I = 0.89$). Both of these values fall within the range of other intraspecific identity values obtained for plant populations and are considerably higher than those reported for congeneric species (Gottlieb 1981, $I = 0.67$). Other intraspecific identity values (I) for eragrostoid grasses reported are: 0.96 for *Bealia mexicana*; 0.94 for *Chaboissaea atacamensis*; 0.82 for *C. ligulata*; 0.88 for *C. subbiflora*; 0.95 for *Muhlenbergia argentea*; 0.98 for *M. lucida*; and 0.93 for *Scleropogon brevifolius* (Peterson and Columbus 1997; Peterson and Herrera A. 1995; Peterson et al. 1993). Because there was a single unique allele present in the South American populations where less genetic variation exits and these same populations were missing six alleles found in North American populations, it seems likely that *Lycurus setosus* has recently dispersed to the Southern hemisphere.

Scleropogon brevifolius (Peterson and Columbus 1997) and *Muhlenbergia torreyi* (Kunth) Hitchc. (Peterson and Ortiz, in preparation) apparently have similar biogeographical histories. Like *Lycurus setosus,* populations of both species have lower levels of genetic variation in the Southern hemisphere and have very few or no unique alleles while lacking alleles shared by North American populations. This North to South American dispersal is seen in *Chaboissaea,* where a single species or vicariad, *C. atacamensis,* has recently dispersed from Mexico to South America from its closest sister, *C. ligulata* (Sykes et al. 1997). The north to south migration pattern is not always the case, and the reverse (south to north) is exhibited in *Bothriochloa* Kuntze

(Allred 1981) and *Erioneuron* Nash (Peterson in preparation). *Chaboissaea, Lycurus,* and *Muhlenbergia,* all members of subtribe Muhlenbergiinae, have centers of diversity in North America. In contrast, *Erioneuron,* a member of the Munroinae (including *Blepharidachne* Hack., *Dasyochloa* Willd. ex Rydb., and *Munroa* Torr.) has a center of diversity in South America. Two major themes that all of these disjunctions seem to have in common is 1) recent migration, since little morphological differences and very little genetic differentiation exist, and 2) the putative dispersed species or taxon has migrated away from a center of diversity.

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Literature cited

Allred, K. 1981. Cousins to the south: amphitropical disjunctions in Southwestern grasses. Desert Plants 3:98–106.

Avdulov, N. P. 1931. Karyo-systematische Untersuchungen der Familie Gramineen. Bulletin of Applied Botany and Plant Breeding Supplement 44:1–428.

Beal, W. J. 1896. Grasses of North America. Vol. 2. Henry Holt & Company, New York.

Clayton, W. D. 1975. Chorology of the genera of Gramineae. Kew Bulletin 30:111–130.

——— and S. A. Renvoize. 1986. Genera Graminum. Grasses of the world. Her Majesty's Stationary Office, London.

Duvall, M. R., P. M. Peterson, and A. H. Christensen. 1994. Alliances of *Muhlenbergia* (Poaceae) within New World Eragrostideae are identified by phylogenetic analysis of mapped restriction sites from plastid DNAs. American Journal of Botany 81:622–629.

Gottlieb, L. D. 1981. Electrophoretic evidence and plant populations. Progress in Phytochemistry 7:1–46.

———. 1982. Conservation and duplication of isozymes in plants. Science 216:373–380.

Gould, F. W. 1964. Documented chromosome numbers of plants. Madroño 17:267.

———. 1965. Chromosome numbers in some Mexican grasses. Boletin de la Sociedad Botanica de Mexico 29:49–62.

Hamrick, J. L. and M. J. W. Godt. 1989. Allozyme diversity in plant species. Pp. 43–63 *in* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.), Plant population genetics, breeding and genetic resources. Sinauer Associates Inc., Sunderland, MA.

———, Y. B. Linhart, and J. B. Minton. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annual Review of Ecology and Systematics 10:173–200.

Hartley, W. and C. Slater. 1960. Studies on the origin, evolution, and distribution of the Gramineae. III. The tribes of the subfamily Eragrostoideae. Australian Journal of Botany 8:256–276.

Hitchcock, A. S. 1913. Mexican Grasses in the United States National Herbarium. Contributions to the U.S. National Herbarium 17:181–389.

———. 1937. *Lycurus* H. B. K. North American Flora 17:542.
———. 1939. *Lycurus* H. B. K. North American Flora 17:543.
JAIN, S. K. and P. L. WORKMAN. 1967. Generalized F-statistics and the theory of inbreeding and selection. Nature 214:674–678.
KUNTH, C. S. *In* F. W. H. A. von Humboldt, A. Bonpland, and C. S. Kunth. 1816. Nova Genera et Species Plantarum. Gramineae. Vol. 1 (pts 1–4):1–377.
MEZ, C. 1921. Gramineae novae vel minus cognitae. Repertorium Specierum Novarum Regni Vegetabilis 17:203–214.
MORDEN, C. W., J. DOEBLEY, and K. F. SCHERTZ. 1987. A manual of techniques for starch gel electrophoresis of *Sorghum* isozymes. Texas Agricultural Experiment Station, MP-1635, College Station.
NEI, M. 1972. Genetic distance between populations. American Naturalist 106:283–292.
NUTTALL, T. 1848. Descriptions of plants collected by Mr. William Gambel in the Rocky Mountains and Upper California. Proceedings of the Academy of Philadelphia 4:7–26.
PETERSON, P. M. and C. R. ANNABLE. 1991. Systematics of the annual species of *Muhlenbergia* (Poaceae-Eragrostideae). Systematic Botany Monographs 31:1–109.
——— and J. T. COLUMBUS. 1997. Allelic variation in the amphitropical disjunct *Scleropogon brevifolius* (Poaceae: Eragrostideae). BioLlania, special edition 6: 473–490.
———, M. R. DUVALL, and A. H. CHRISTENSEN. 1993. Allozyme differentiation among *Bealia mexicana, Muhlenbergia argentea,* and *M. lucida* (Poaceae: Eragrostideae). Madroño 40:148–160.
——— and Y. HERRERA A. 1995. Allozyme variation in the amphitropical disjunct *Chaboissaea* (Poaceae: Eragrostideae). Madroño 42:427–449.
———, R. D. WEBSTER, and J. VALDES-REYNA. 1995. Subtribal classification of the New World Eragrsotideae (Poaceae: Chloridoideae). Sida 16:529–544.
———, ———, and ———. 1997. Genera of New World Eragrostideae (Poaceae: Chloridoideae). Smithsonian Contributions to Botany 87:1–50.
PILGER, R. 1954. Das System der Gramineae. Botanische Jahrbücher 76:281–384.
———. 1956. Gramineae. *In* Die Natürlichen Planzenfamilien, ed. 2. 14d. 168pp.
REEDER, C. G. 1985. The genus *Lycurus* (Gramineae) in North America. Phytologia 57:283–291.
REEDER, J. R. 1967. Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bulletin of the Torrey Botanical Club 94:1–17.
———. 1971. Notes on Mexican grasses IX. Miscellaneous chromosome numbers—3. Brittonia 23:105–117.
———. 1977. Chromosome numbers in western grasses. American Journal of Botany 64:102–110.
SÁNCHEZ, E. and Z. RÚGOLO DE AGRASAR. 1986. Estudio taxonómico sobre el genero *Lycurus* (Gramineae). Parodiana 4:267–310.
SWOFFORD, D. L. and R. B. SELANDER. 1989. *Biosys*-1, a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. University of Illinois, Urbana.
SYKES, G. R., A. H. CHRISTENSEN, and P. M. PETERSON. 1997. A chloroplast DNA analysis of *Chaboissaea* (Poaceae: Eragrostideae). Systematic Botany (in press).
VALDES-REYNA, J. and S. L. HATCH. 1991. Lemma micromorphology in the Eragrostideae (Poaceae). Sida 14:531–549.
WEEDEN, N. F. and J. F. WENDEL. 1989. Genetics of plant isozymes. Pp. 46–72 *in* D. E. Soltis and P. S. Soltis (eds.), Isozymes in plant biology. Dioscorides Press, Portland, OR.
WRIGHT, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395–420.
———. 1969. Evolution and genetics of populations. Vol. 2, The theory of gene frequencies. University of Chicago Press, Chicago.
———. 1978. Evolution and genetics of populations. Vol. 4, Variability within and among natural populations. University of Chicago Press, Chicago.

APPENDIX 1. Allele frequencies for 13 populations of *Lycurus setosus* (see Table 1 for population localities) from North and South America. Unique alleles found in a single individual are marked with an asterisk.

	POPULATIONS												
	SOUTH						NORTH						
LOCUS	11439	11513	11622	11724	11746	11762	12174	12184	12218	12246	12299	12320	12350
AAT-1													
A	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
B	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
AAT-2													
A	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
B	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
ACO-1													
A	.000	.032	.019	.121	.000	.000	.018	.000	.259	.250	.125	.074	.978
B	.000	.000	.241	.172	.000	.000	.018	.000	.019	.000	.000	.000	.022
C	1.000	.968	.741	.707	1.000	1.000	.964	1.000	.722	.750	.875	.926	.000
ACO-2													
A	1.000	.984	1.000	.500	.500	.850	1.000	1.000	.907	.500	.732	.778	.196
B	.500	.016	.000	.500	.500	.000	.000	.000	.093	.500	.268	.222	.043
C	.000	.000	.000	.000	.000	.150	.000	.000	.000	.000	.000	.000	.761
AMP-1													
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AMP-2													
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GDH													
A	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
B	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500

APPENDIX 1. Continued.

	POPULATIONS												
	SOUTH						NORTH						
LOCUS	11439	11513	11622	11724	11746	11762	12174	12184	12218	12246	12299	12320	12350
GPT													
A	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
B	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500
IDH													
A	.500	.032	.407	.466	.217	.083	.500	.446	.296	.393	.214	.259	.043
B	.500	.968	.537	.500	.650	.883	.000	.196	.611	.107	.786	.444	.957
C	.000	.000	.056	.034	.133	.033	.500	.357	.093	.500	.000	.296	.000
PGD													
A	.500	.500	.500	.500	.500	.500	.000	.500	.056	.500	.000	.167	.000
B	.500	.500	.500	.500	.500	.500	1.000	.500	.944	.500	1.000	.833	1.000
PGI-1													
A	.000	.000	.000	.000	.000	.000	.500	.500	.500	.500	.500	.500	.500
B	.000	.016*	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.500	.484	.500	.500	.500	.500	.000	.089	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.446	.411	.389	.500	.375	.444	.500
E	.500	.484	.500	.500	.500	.500	.036	.000	.000	.000	.000	.000	.000
F	.000	.016	.000	.000	.000	.000	.018	.000	.111	.000	.125	.056	.000
PGI-2													
A	.000	.048	.167	.190	.000	.033	.000	.464	.000	.089	.037	.000	.000
B	.500	.452	.333	.310	.500	.467	.500	.000	.500	.411	.463	.500	.500
C	.000	.000	.000	.000	.000	.000	.000	.036*	.000	.000	.000	.000	.000
D	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500	.500

Appendix 1. Continued.

	Populations												
	South						North						
Locus	11439	11513	11622	11724	11746	11762	12174	12184	12218	12246	12299	12320	12350
PGM-1													
A	.000	.032	.000	.000	.000	.033	.018	.500	.241	.071	.000	.000	.022
B	1.000	.968	1.000	1.000	1.000	.967	.982	.500	.759	.929	1.000	1.000	.978
PGM-2													
A	.000	.000	.500	.500	.500	.467	.500	.000	.222	.500	.250	.037	.696
B	1.000	1.000	.500	.500	.500	.533	.500	1.000	.778	.500	.750	.963	.304
SAD-1													
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.174*
B	.500	.500	.500	.000	.300	.000	.500	.536	.019	.571	.250	.537	.326
C	.500	.500	.500	1.000	.700	1.000	.500	.464	.981	.429	.750	.463	.500
SAD-2													
A	.500	.968	.500	.655	.500	.500	.125	.464	.481	.875	.768	.750	.478
B	.500	.000	.500	.345	.000	.500	.821	.536	.167	.125	.232	.250	.478
C	.000	.000	.000	.000	.000	.000	.054	.000	.000	.000	.000	.000	.022
D	.000	.032	.000	.000	.500	.000	.000	.000	.130	.000	.000	.000	.022
TPI-1													
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.019*	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.981	1.000
TPI-2													
A	.000	.032	.000	.000	.500	.150	.000	.500	.500	.500	.000	.093	.065
B	1.000	.968	1.000	1.000	.500	.850	1.000	.500	.500	.500	1.000	.907	.935